

GENERIC CONSIDERATIONS CONCERNING CARPHEPHORUS AND TRILISA (COMPOSITAE)

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The genus *Carphephorus* (Greek: karphe: chaff, and phoros: bearing) was established by Henri Cassini (1816). In describing this genus, Cassini stated that it differed from *Liatris* "par le clinanthe muni de grandes squamelles comme les calea, et par l'aigrette nonplumeuse" and consequently named the species *Carphephorus pseudoliatris*; in 1817, he placed *Carphephorus* near *Liatris*, in the natural tribe Eupatorieae.

In 1818, Cassini also erected the subgenus *Trilisa* which he elevated to generic rank in 1820 when he placed it with 15 other genera in the Eupatorieae. In establishing *Trilisa*, he stressed that it had the greatest affinity with *Carphephorus* from which it differed by the naked receptacle, but he was also careful to point out that *Trilisa odoratissima* "portoit accidentellement quelques squamelles". This last remark has been a central point of controversy over the generic limits of *Carphephorus* and *Trilisa*. No species were actually transferred to *Trilisa* until 1828, when Cassini cited *Liatris odoratissima* and *Liatris paniculata* of Willdenow (1803) as species of *Trilisa*. However, the genus *Trilisa* was not accepted at once, De Candolle (1836) and Torrey and Gray (1841) used it as a sectional name of the genus *Liatris*, but Bentham and Hooker (1873) referred to the incorrect use of Cassini's generic name for a section.

Carphephorus was thought to be of Siberian origin until Torrey and Gray (1841), prompted by a remark of Chapman, found that the chaffy receptacle had been overlooked by some botanists in describing other species and rightly recognized that *Carphephorus* referred to American plants. Consequently they proceeded to transfer *Liatris bellidifolia*, *Liatris tomentosa* and *Liatris corymbosa* to *Carphephorus*.

In 1924, the monotypic genus *Litrisa* (anagram of *Trilisa*) was described by Small for an endemic plant of Central

Florida. He concluded his description with the following remark: "Technically it is most closely related on the one hand to *Trilisa*, by its involucre, and on the other, to *Carphephorus*, by its chaffy receptacle." Apparently Small contradicted himself, because in his flora (page 1304, 1933) he keyed out *Litrise* as having a naked receptacle. Robinson (1934) noticing the contradiction, examined the type as well as other material and apparently not finding any pales, he decided to transfer *Litrise* to *Trilisa* rather than *Carphephorus*, implying as it had been customary, that *Trilisa* has no pales. So in addition to *T. odoratissima* and *T. paniculata*, a third species *carnosa* was added to the small genus *Trilisa*.

C. W. James (1958), upon examination of the three species of *Trilisa*, found that pales may be borne in any one of them and decided to merge at least *Trilisa carnosa* with the genus *Carphephorus*, using as primary generic distinction, the imbrication of the phyllaries. As the other two species had generally non-imbricate phyllaries, he considered that it was better "at the present time" to keep them in the segregate genus *Trilisa*.

The taxonomic discrepancies encountered in the *Carphephorus-Litrise-Trilisa* complex cannot be attributed to thoughtless "splitting" or "lumping" but to incomplete information and inconsistent primary generic characters. Already in 1913, Robinson had noted in his studies of the Eupatorieae, that it is probable that "when these genera are more satisfactorily represented in herbaria some new and more convincingly natural re-adjustment of generic lines will become possible."

Bearing in mind that "fundamental" or "key" character can lead to misplacement of taxa, and that "every taxonomic character is potentially important" (Cronquist, 1957), a careful analysis of all available data was made. As the degree of relation may be determined by the "scientific" use of morphological similarity, a statistical evaluation of various characters that are "repeatable and verifiable" (Davidson, 1963) was attempted to corroborate the results

obtained. The validity of this approach is based upon the premise that "similar or identical genetic systems operate to produce similar or identical phenotypes, always of course, allowing for the effects of the environment. If two plants have similar structures throughout, they are related." (Rollins, 1953)

The survey revealed a very close relationship between all seven species under consideration.

a) Karyotype: The cytological studies have yielded no evidence for the maintenance of the two species of *Trilisa* as distinct from *Carphephorus*. All seven species have $2n = 20$. The karyotypes of *Trilisa odoratissima* and *Trilisa paniculata* have been found "to be indistinguishable from that of *Carphephorus*." (Gaiser, 1954). The seven species apparently have:

- 1 pair of long chromosomes with a median constriction
- 1 pair of long chromosomes with a submedian constriction
- 1 pair of long chromosomes with a subterminal constriction
- 3 pairs of chromosomes of median length with a median constriction
- 1 pair of chromosomes of median length with a submedian constriction
- 2 pairs of chromosomes of median length with a subterminal constriction
- 1 pair of short chromosomes with a median constriction.

These chromosomal similarities are particularly significant, because most of the other members of the Kuhninae have chromosomes which differ either in shape and/or in number.

So far as known the species are perfectly distinctive, present relatively little variation and do not intergrade at all with others; interspecific hybridization has not been reported, in spite of overlapping ranges, similarities of habitats and coinciding flowering times. It is to be noted

that *Carphephorus* populations have generally a limited number of individuals and do not cover a wide area.

b) Distribution: The geographical distribution is a natural one; the seven species are confined to the southeastern coastal plain of the United States, generally on dry pine barrens.

c) Habit: All are perennial caulescent herbs with a non-deciduous rosette of basal leaves and alternate cauline leaves decreasing in size upwards. The blades are entire or shallowly toothed.

d) Basal leaves: Except for *Carphephorus pseudoliatris*, the basic pattern of the basal leaves is oblanceolate or spatulate. The ratio: maximal width of distal part/width of proximal part (measured at the quarter of the total length of the leaf) shows that the range of variation is approximately the same; only *C. pseudoliatris* and *C. carnosus* have less variation, the first having acicular leaves, the second, leaves tending to be linear-lanceolate. The ratio: maximal length/maximal width is not very significant due to the great variation of the length of the leaves.

e) Pubescence: The pubescence has been found to be of use as a character for specific differentiation between *C. tomentosus* and *C. bellidifolius* and between *T. paniculata* and *T. odoratissima*. The trichomes are generally non-glandular, multicellular, uniseriate, cylindrical, tapering towards the end and variable in length; in *T. paniculata*, the trichomes are biseriate.

The glandular trichomes are generally present in depressions below the epidermal surface and cause the characteristic punctation. These trichomes are biseriate in *C. carnosus* and *C. tomentosus*, and in the latter they are accompanied by laterally placed uniseriate filaments. They are uniseriate in the five other species (and occasionally also in *C. carnosus*) and usually occur singly, but in *C. pseudoliatris* and *C. corymbosus* they can also be found in groups of 2, 3 or 4. As noted by Gaiser (1954), a very reticulate pattern is evident in the distribution of the glandular trichomes.

f) Inflorescence: All species have the same basic cymose type of inflorescence, the heads being arranged in a corymbose fashion in six species, and in a racemose fashion in *T. paniculata*. The cymes are contracted in *C. pseudoliatris* and *C. carnosus*, and spreading in the other species.

g) Flowers: The number of flowers per head varies from 4 in *T. paniculata* to 46 in *C. pseudoliatris*. In the related genus *Liatris*, it varies from 3 to 70 (Gaiser, 1946). The floral parts are identical in all species. Their size varies but the range is not abnormal for a genus. The corolla for example, varies from 3.4 mm to 11 mm in this complex, while in *Liatris*, it varies from ca. 5 mm to ca. 20 mm (Gaiser, 1946). The corolla lobes show also a normal gradation in length, being longest in *C. bellidifolius* (Mean: 2.286 mm) and shortest in *C. carnosus* (Mean: 0.723). The anthers are definitely shorter in *C. carnosus*, *T. odoratissima* and *T. paniculata* than in the four other species. The apical end of the anthers is scarious in the seven species, but notched in only five of them: *C. pseudoliatris*, *C. tomentosus*, *C. bellidifolius*, *C. corymbosus* and *C. carnosus*.

h) Pappus: The bristles being of unequal length on each fruit, the overall length of the pappus was obtained by measuring the longest bristles. There is a variation from 3 to 10 mm, while in the genus *Liatris* it varies from 2.5 to 10 mm (Gaiser, 1946). The bristles generally number 30-55; in *T. odoratissima* they number 20-35.

i) Achenes: They are basically alike, being 10-ribbed, angular and narrowed towards the base. The mature achenes are of brown color, but in some cases they approach black. The length varies from 2 to 7 mm; in *Liatris* it varies from 3 to 10 mm (Gaiser, 1946).

j) Phyllaries and pales:

(1) Shape and size: The margin of phyllaries has proved to be a useful specific character; the margin can be pectinate-ciliate, erose-ciliate, eciliate or scarious; the apex also, varying from acute, mucronate to obtuse or rounded, is characteristic; on the other hand, characters like shape, width, length or pubescence vary much within

each species and can rarely be used as distinctive characters. It is to be noted that the pales generally resemble the inner phyllaries in shape, pubescence and size; occasionally, they are much narrower than the phyllaries.

(2) Number: The pales and the phyllaries which have been used as primary generic characters, show apparently a great range of numerical variation. But as the number of flowers per head varies much also, that range presents nothing unusual. For example, *C. pseudoliatris* which may have up to 46 flowers in one head has a mean number of pales of 23 and a mean number of phyllaries of 20; *T. paniculata* which often has only 4 flowers in one head has a corresponding low mean number of pales, 0.15 per head, and a mean number of phyllaries of 6.2 per head. It seems that the number of phyllaries and pales is related to the number of flowers. If one considers that the phyllaries and the pales are homologous — this is in accord with the theory of formation of the capitulum from an ancestral racemose umbel (Small, 1919) — a correlation can be seen between the number of phyllaries and pales (considered together) and the number of flowers. An increase in one set is matched by an increase in the other set; *T. paniculata* and *C. carnosus* which have the smallest number of flowers have also the smallest number of pales and phyllaries while *C. pseudoliatris* which has the greatest number of flowers has also the greatest number of pales and phyllaries. On the other hand, a statistical attempt to relate the number of flowers and either the number of pales or the number of phyllaries gave negative results, especially in the case of *C. pseudoliatris* which seems to possess too many pales and too few phyllaries. This stems from the difficulty of delimiting the pales and the phyllaries; in fact, no sharp line can be drawn between them, their position being often very indefinite and their shape identical. As a control, one species of *Liatris* has also been plotted and apparently does not contradict the theory that there is a correlation between flower-number and pale-phyllay-number. So, in the complex under consideration, it appears

sound to consider phyllaries and pales as a whole, because their structure is generally indistinguishable and seems to be controlled by the same genetic factor.

From these considerations, it is normal to expect fewer pales in a small head or even none, the flowers being almost all peripheral in position; thus, it would be an inadvisable decision to segregate *T. odoratissima* and *T. paniculata* simply because one fails to see pales in some heads. In the case of *T. odoratissima*, the pales were constantly seen in the plants I collected in September 1965, as well as in most herbarium specimens examined. Unfortunately no fresh material of *T. paniculata* could be examined and the herbarium specimens showed a great paucity of pales. However, James who had more opportunities of observing fresh material wrote in 1958: "Upon examination of all the species of the genera under consideration, I conclude that pales may be borne in any one of the species." As the pales are deciduous and tend to fall off when they are dry, it is possible that the "*odoratissima*" specimen examined by Cassini (1820) had lost most of its pales; that would have prompted Cassini to establish a distinction between *Carphephorus* and *Trilisa* and to write that "*Les Trilisa ont la plus grande affinité avec le Carphephorus, qui n'en diffère que par le clinanthe squamellifère; et j'ai observé sur la Trilisa odoratissima que le clinanthe portoit accidentellement quelques squamelles.*" It is also possible that, finding only one or two pales in each head, or sometimes none, he concluded that the pales are not a permanent feature and occur only occasionally. At any rate, his word "accidentellement" is definitely too strong and conveys an erroneous idea about the presence of pales in *T. odoratissima*. Presumably, if Cassini had examined some fresh material, he would have merged *Trilisa* with *Carphephorus*, because he was not impressed by other differences. These considerations show how the exclusive use of the "presence of pales" is questionable as a primary generic criterion. As E. E. Sherff has pointed out: "There should not be separation of genera solely upon the presence or absence of one or

more supposedly diagnostic characters." (Reported by Turrill, 1942). This principle is particularly valuable in this case where the state of maturity of the plant can affect the character under consideration.

(3) Imbrication of phyllaries: The imbrication of phyllaries used by James to segregate "much more naturally" *Trilisa odoratissima* and *Trilisa paniculata* from *Carphephorus* is considered to be on a very weak basis (Shinners, 1946), especially when it is not supported by additional characters. Besides, it presupposes a sharp line where none can be drawn. In this complex, a gradation from 1 to 5 series of phyllaries is found. As the number of series is dependent on the number of phyllaries, it is evident that when the phyllaries number only 4 or 5 they can hardly overlap and be imbricated. So the imbrication of phyllaries is simply a qualitative factor based on quantitative data and cannot be taken as a distinctive character in itself. Upon examination of numerous specimens, I found that the number of series is highest in *C. tomentosus* and lowest in *T. paniculata*. But, for each species, the number varies and no line of demarcation can be set between them. Robinson (1934) had come to the same conclusion when he merged *Litrisa* with *Trilisa*: "The alleged involucral difference appears in fact a rather vague one of degree only."

Too much emphasis and exclusive reliance placed upon either the amount of pales or the arrangement of phyllaries has led to different results and varied segregation, but when the plants are considered as a whole and not as an aggregate of uncorrelated features, I find no solid ground to keep *Trilisa* as a separate genus. To maintain *Trilisa* distinct from *Carphephorus*, "because of tradition and inertia" (McVaugh, 1945) would impede a better understanding of their fundamental relationship and conserve an unwarranted segregation.

The generic transfer of *Trilisa* I propose is somewhat similar to the case of *Hymenopappus*. That genus had been placed in the tribe Helenieae, because the heads have no chaff; recent investigations showed that *Hymenopappus*

was not only more naturally placed in the Anthemideae, close to its obviously related prototype, the chaffy *Leucampyx*, but had to be united into a single genus, on the basis of the total data (Turner, 1956); since then the genus *Hymenopappus* includes "everything from perennial plants with chaffy receptacle and rayed heads to biennials with neither chaff nor rays." (Turner, 1956). With the transfer of both species of *Trilisa*, *Carphephorus* remains a homogeneous genus, much more than *Hymenopappus*, *Liatris* and many other composite genera. Only *T. paniculata* with its few pales, its rarely imbricate phyllaries and its cyme arranged in a paniculate fashion, would be slightly anomalous but would hardly alter the generic limits. Thus, if one compares the range of variation of the *Carphephorus-Trilisa* complex with the one of *Liatris*, one finds that there is no justification to keep *Trilisa* as a distinct genus. In fact, it is significant that *Liatris* which has been studied thoroughly by Robinson and Gaiser has not been split in spite of the numerous variations observed. There is no reason to consider *Carphephorus* a fundamentally different case. As pointed out by Blackwelder "group which cannot be distinguished at any particular level by the characters used for their neighbors must be combined at that level." (1963)

As I find that the biological status of all the species concerned may be best expressed by the grouping of all into one genus, I must follow the only alternative of uniting *Trilisa* to *Carphephorus*. This more comprehensive genus conforms to the definition of a genus given by Buxbaum (1951), as "the sum total of species belonging to a phylogenetic unit recognized as such by the unity of its morphological type." It is also in accord with Recommendation 3 of McVaugh (1945): "The most important criterion of any supposed genus is not the width of the gap between it and another, but its own biological unity. Homogeneity in many characters, regardless of the degree of overlapping of these characters with those of other genera, is the best indicator of this unity." No

doubt that those who like to make far too fine generic segregations will find that such a group is a return to the broad concept of genus in folk botany; these forget that "large genera may be quite as truly 'entities of nature' as small ones, . . . and from a practical and linguistic standpoint may be a far more useful concept." (Bartlett, 1940).

Carphephorus odoratissimus (J. F. Gmel) Hebert, comb. nov. based on *Chrysocoma odoratissima* J. F. Gmel, Syst. 2: 1204. 1792. Type: preserved in John Fraser's collection, in the British Museum, London. Place of origin: Carolina.

Carphephorus paniculatus (J. F. Gmel) Hebert, comb. nov. based on *Chrysocoma paniculata* J. M. Gmel, Syst. 2: 1204. 1792. Type: preserved in John Fraser's collection, in the British Museum, London. Place of origin: Carolina. Isotype: Lamarck Herbarium, Paris.

KEY TO THE SPECIES.

- a) Heads with 12-43 flowers; pales 4-33 per head; phyllaries 12-33 per head; involucres 6-11 mm high.
 - b) Basal leaves acerose, involute. 1. *C. pseudoliatris*.
 - b) Basal leaves oblanceolate or spatulate, not involute.
 - c) Phyllaries pubescent, their margins pectinate-ciliate. 2. *C. tomentosus*.
 - c) Phyllaries glabrous or minutely hairy, their margins erose- or suberose-ciliate.
 - d) Inflorescence an open slenderly-branched cyme; corolla lobes ca. 2-3 mm long. 3. *C. bellidifolius*.
 - d) Inflorescence a dense compact corymbose cyme; corolla lobes ca. 1 mm long. 4. *C. corymbosus*.
- a) Heads with 3-12 flowers; pales (0-) 1-3 per head; phyllaries 4-14 per head; involucres 3-6 mm high.
 - e) Inner phyllaries pubescent, with pectinate-ciliate margins. 5. *C. carnosus*.
 - e) Inner phyllaries glabrous, with eciliate margins.
 - f) Stems glabrous; inflorescence an open and spreading corymbose cyme. 6. *C. odoratissimus*.
 - f) Stems sparingly hirsute, viscid; inflorescence a thyrsoid panicle. 7. *C. paniculatus*.

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SPIRANTHES OVALIS. NEW FOR KANSAS

While collecting in an oak-hickory woodland 2 miles north and $\frac{3}{4}$ mile east of Baldwin City, Douglas County, Kansas, a specimen of *Spiranthes ovalis* Lindl. was taken on October 13, 1967 (*Johnson 1184*, KANU). The plant was associated with *Botrychium dissectum* Spreng. var. *obliquum* (Muhl.) Clute, *Corallorhiza odontorhiza* (Willd.) Nutt., and *Monotropa uniflora* L. This orchid has previously been reported from Florida to Texas, north to Virginia Kentucky, Indiana, and Missouri. In Missouri the species is known only from Mississippi, St. Louis, and Jackson Counties. My collection is an extension westward of the range of the species.

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